

Short note

# Why behavioural responses may not reflect the population consequences of human disturbance

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## Abstract

The effect of human disturbance on animals is frequently measured in terms of changes in behaviour in response to human presence. The magnitude of these changes in behaviour is then often used as a measure of the relative susceptibility of species to disturbance; for example species which show strong avoidance of human presence are often considered to be in greater need of protection from disturbance than those which do not. In this paper we discuss whether such changes in behaviour are likely to be good measures of the relative susceptibility of species, and suggest that their use may result in confusion when determining conservation priorities. © 2000 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

A widely studied issue in conservation biology is the potential impact of human disturbance on animal populations (Stalmaster and Newman, 1978; Bélanger and Bédard, 1989; Stockwell et al., 1991; Pfister et al., 1992; Reijnen et al., 1995; Andersen et al., 1996; Gill et al., 1996). Assessments of whether disturbance affects a population, and how severe that effect is, currently rely on proximate measures of the impact of disturbance; usually the behavioural response of the species in question to human presence. Thus, many studies have demonstrated that animals will avoid areas where humans are present (Stalmaster and Newman, 1978; Burger, 1981; Tuite et al., 1984; Sutherland and Crockford, 1993; Klein et al., 1995; Reijnen et al., 1995; Gill, 1996; Gander and Ingold, 1997) and that some species show a greater degree of avoidance than others (Cooke, 1980; Burger and Gochfield, 1991; Smit and Visser, 1993; Rodgers and Smith, 1995). These data have then been suggested as a means of assessing conservation

priorities with respect to the impact of disturbance on populations (Burger, 1981; Tuite et al., 1984; Klein et al., 1995).

For example, a great deal of attention has been given to the impact of disturbance on waterfowl species such as wigeon (*Anas penelope*). This is because of the tendency of such species to show strong avoidance of humans (Tuite et al., 1984, Mayhew, 1988; Madsen, 1995), the huge local decreases in number that can occur when disturbance has increased (Hirons and Thomas, 1993) and the increases in number observed when disturbance is removed from sites (Madsen, 1998). By contrast, species which do not avoid disturbed areas are often considered as requiring little or no protection from disturbance. Thus, Klein et al. (1995) present data on the extent to which different bird species avoid human presence, and conclude that species showing the greatest avoidance require the greatest amount of protection. Similarly, Burger (1981) found differences in the redistribution in response to humans between gulls, wildfowl and shorebirds and suggested that, as shorebirds showed the greatest avoidance, they were the most vulnerable and human activity should be restricted around areas with shorebirds. Tuite et al. (1984) assessed the extent to which numbers of different species of

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waterfowl were reduced by the presence of recreational activities on lakes and concluded that disturbance was an important issue for those species whose numbers were lower than expected but not for those species whose numbers did not change.

From a conservation perspective, human disturbance of wildlife is important only if it affects survival or fecundity and hence causes a population to decline. It is therefore vital for conservationists to know whether avoidance of disturbance does in fact result in population change (Sutherland, 1996; Sutherland, 1998; Gill and Sutherland, 2000). In this paper we discuss whether avoidance of disturbance is likely to be a good measure of population-level effects and suggest that the use of avoidance and other behavioural measures of the impact of disturbance, may result in confusion when determining conservation priorities.

## 2. Why avoidance of disturbance need not reflect population-level consequences

The decision of whether or not to move away from disturbed areas will be determined by factors such as the quality of the site currently being occupied, the distance to and quality of other suitable sites, the relative risk of predation or density of competitors in different sites and the investment that an individual has made in a site (for example, in establishing a territory, gaining dominance status or acquiring information). This is conceptually identical to the well accepted idea that the decisions made by animals of whether to move in response to predation risk depend on the availability and quality of other sites (e.g. Ydenberg and Dill, 1986). The response of animals to predation risk is exactly the same as the response to disturbance; a species with suitable habitat nearby may avoid disturbance simply because it has alternative sites to go to. By contrast, animals with no suitable habitat nearby will be forced to remain despite the disturbance, regardless of whether or not this will affect survival or reproductive success. This will also mean that avoidance behaviour may vary both temporally and between locations, depending on the prevailing local conditions.

Fig. 1 illustrates how the argument that species which show the greatest avoidance of disturbance are also the most vulnerable can be turned on its head. The relationship between disturbance and the relative number of animals across sites is shown for two different levels of availability of alternative habitat and fitness costs of disturbance (i.e. the decline in survival or reproductive success that will result from exposure to disturbance). Species with little suitable habitat available elsewhere (Fig. 1c and 1d) cannot show marked avoidance of disturbance even if the fitness costs are high, whereas species with many alternative sites to move to (Fig. 1a and

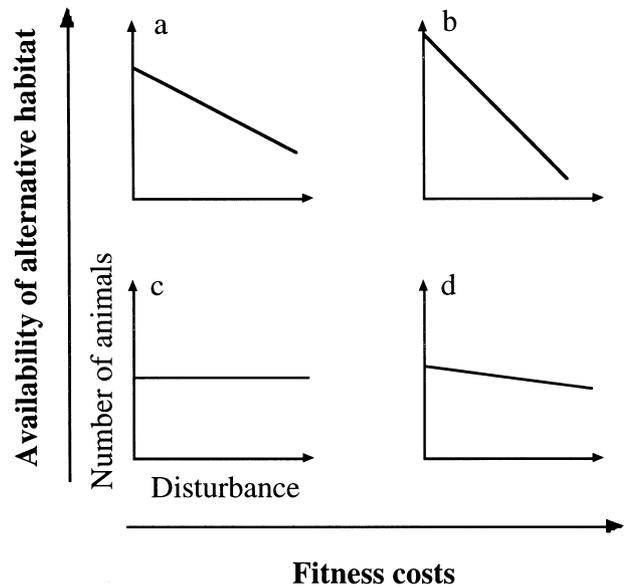


Fig. 1. The effects of increasing fitness costs of disturbance (i.e. increasing mortality or decreasing reproductive success) and availability of alternative habitat, on the distribution of animals across sites varying in disturbance levels. Four scenarios (a–d) are presented showing how the relative number of animals across sites varies with the degree of disturbance in those sites. If the fitness costs of disturbance are high (b and d), individuals move away from disturbed sites and hence numbers are lower in sites with greater disturbance. Similarly, a high availability of alternative habitat elsewhere (a and b), allowing individuals to move readily, will result in a strong decrease in numbers in disturbed sites, even when the fitness costs of disturbance are low (a). If there is little excess habitat to move to (c and d), there will be little change in numbers with increasing disturbance, even if there is a large fitness cost in terms of reduced survival or fecundity (d).

1b) are likely to avoid disturbance even if the fitness costs are low. Traditionally, species showing strong negative relationships (e.g. Fig. 1a and b) would be considered to be those most in need of protection from disturbance. However, the figure shows that this response could in fact be the result of differences in the availability of habitat elsewhere. Thus, species may be able to avoid disturbance because they have alternative sites to go to. By contrast, species may not avoid disturbance because they have no other sites to occupy. From a population viewpoint, the species most likely to be adversely affected by disturbance are those for which the fitness costs are high but they have little excess habitat to move to (e.g. Fig. 1d) and are thus constrained to stay in disturbed areas and to suffer the costs in terms of reduced survival or reproductive success.

For example, as described earlier, many waterfowl species show strong avoidance of disturbance. However, such species are often herbivorous and feed in dense flocks on a wide range of short swards. For these species, the costs of moving to an alternative site are, therefore, likely to be small as there are likely to be similar sites nearby. In addition, such species are often

hunted and so the costs of not moving in response to human presence could potentially be severe. By contrast, for species that feed on mobile or highly aggregated prey, the costs of moving to alternative sites may be great, especially if they are territorial or experience high levels of interference competition. Such species could then be forced to tolerate disturbance which may or may not affect survival or fecundity and hence population size (e.g. Goss-Custard and Verboven, 1993).

The behavioural process that we have concentrated on here is the avoidance of disturbance, as this is the most commonly used behavioural measure in studies of disturbance. However, exactly the same argument could be made for all other forms of behavioural response to disturbance, for example reduced prey intake rates, increased vigilance levels, reduction in levels of parental care or amount of time spent in flight. Whilst all of these clearly have the potential to affect survival or fecundity, the actual fitness costs of such changes in behaviour need to be quantified before they can be used as reliable estimates of the impact of disturbance on populations.

Assessing the relative importance of disturbance to species by their change in distribution could thus give opposite results to those expected. In particular, species that do not avoid disturbance and are thus assumed not to be vulnerable, for example, the herons, egrets, and pelicans in a Florida nature reserve (Klein et al., 1995) and pochard (*Aythya marila*), tufted duck (*A. fuligula*) and goosander (*Mergus merganser*) on inland waters in the UK (Tuite et al., 1984), could potentially be worthy of equal or greater concern than those that clearly avoid human presence. If the aim is to maintain or increase the numbers of animals using a site, then assessing whether disturbance causes birds to leave would be an appropriate methodology. However, in order to assess the impact of disturbance on population size and the relative susceptibility of different species, future studies need to address how behavioural changes in response to disturbance affect demographic parameters such as survival and reproductive success. This will also require an understanding of the strength of density-dependence within a system, in order to determine whether changes in survival or fecundity will have any impact on overall population size. Field estimates of the strength of density-dependent mortality or fecundity are currently rare, however, as we have shown here, without them it is impossible to assess which species are in need of protection. In the short-term, the most sensible approach may, therefore, be to concentrate research and protection efforts on species that are threatened or whose populations are declining, and for which human disturbance is implicated as a possible cause. Otherwise there is a risk that valuable resources will be spent and human access to wildlife areas will be restricted in order to protect species for which human presence alters behaviour but has no other impact.

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